Pedobiologia **38**, 429–447 (1994)
Gustav Fischer Verlag Jena

Oribatid mites/Diptera interactions in a deciduous forest leaf-litter: an application of multivariate analysis under linear constraints

Alain Bellido and Simone Deleporte

Station Biologique, Laboratoire d'Ecologie du Sol, UA CNRS 1853 F-35380, Paimpont, France

Summary. We hypothezise that the transformation of dead foliar material by Diptera larval action represents a modification of food sources and microhabitats of microarthropods which can be monitored by observing changes in the structure of their communities, and particularly of the oribatid mite community. To test this hypothesis, we compared experimentally in the field oribatid communities from leaves eaten by *Bradysia confinis* sciarid larvae and from uneaten leaves. The detailed analysis at species level, using multivariate methods under linear constraints, highlights the species that respond positively and those that respond negatively to a substrate modified by larval activity. We emphasize the relevance of the multivariate methods to make an accurate typology between these species. Of the 21 species censused in the whole experiment, 10 show significant response with regard to leaf breakdown and allow the construction of a diagrammatic working hypothesis showing the phases of colonization and succession of these oribatid species on decomposing leaf material in a natural situation. *Hermannia gibba*, *Oribatula tibialis* and *Ceratoppia bipilis* appear as interesting species for a study of the relations between transformation of leaf material during degradation and population development.

Key words: Oribatid mites, Sciarid diptera, trophic interactions, deciduous litter, redundancy analysis, succession

Introduction

The role of soil arthropods in the decomposition of leaf-litter is now well established. In addition to numerous experiments in "litter-bags", the most recent studies in microcosm reveal the process of mineralization of nitrogen and carbon in relation to the soil fauna (Anderson & Ineson 1982, 1984; Setälä et al. 1988; Huhta et al. 1991). The breakdown of leaves and their passage through the gut of invertebrates stimulates microfloral activity in the deposited faeces (Nicholson et al. 1966; Anderson et al. 1983; Ineson & Anderson 1985; Gunarsson & Tunlid 1986). Few studies on litter degradation processes concern interactions between several groups, except for Diplopods (Szlavecz & Pobozsny 1993). Futhermore, the most studied soil saprophagous groups are generally earthworms, Collembola and Acarina, whereas Diptera, despite their high abundance, are rarely studied (Deleporte 1981; Borin & Herlitzius 1987). Therefore, our approach is novel, both in the study of fauna/fauna interactions in litter system functioning, and in the zoological groups considered, i.e. Diptera associated with Acarina.

The sciarid *Bradysia confinis* (Winn., Frey 1948), a monovoltine species from deciduous forest leaf-litter, has a period of intense larval feeding activity over two months in W. France

---

Correspondence to: A. Bellido

(February and March) in the L layer of the litter (Deleporte 1986). Leaf consumption can reach 22 $g \cdot m^{-2}$ of dry mass during these two months. The estimated faeces production of 12 $g \cdot m^{-2}$ (dry mass) means that over the same period around 5% of the annual accumulation of litter may be broken down by larvae (Deleporte 1987). In years of high larval density, litter breakdown is such that over these two months the F layer almost disappears. The faeces produced represent a substrate well broken down and chemically transformed by enzymatic activity during gut transit (Deleporte 1988; Deleporte & Rouland 1991), suitable for microfloral development (Ineson & Anderson 1985; Shaw et al. 1991). Larval action transforms the substrate at three levels: fragmentation, chemical transformation and microflora growth stimulation. We hypothesize that this transformation represents a modification of food sources and microhabitats at the community level for microarthropods that can be monitored by observing changes in the structure of their communities, more specially of the oribatid mite community. To test that hypothesis, we compared experimentally in the field oribatid mite communities from leaves eaten by *B. confinis* larvae and from uneaten leaves. We emphasize the use of a new multivariate analysis that is particularly effective at assessing species ordination.

Materials and Methods

The study site

The study site is located in the forest of Paimpont (Brittany, France). It is a 20–30 year-old mixed coppice of *Quercus sessiliflora* Salisb., *Quercus pedunculata* Ehrh. and *Fagus sylvatica* L., with a few *Pinus sylvestris* L. and *Castanea sativa* Mill. There is a discontinuous dwarf-shrub layer of *Vaccinium myrtillus* L. The annual accumulation of leaf litter is around 330 $g \cdot m^{-2}$ (dry mass). Humus pH is around 4.5. The region has a cool, damp, oceanic climate.

Experimental procedure

Preparation of leaf material: Oak leaves which fell during the period 15 October – 30 November 1982 were collected on March 1 1983. They had therefore already been subjected *in situ* to leaching by rain and to the action of microorganisms. In the laboratory they were air dried, carefully brushed to remove leaf fragments and other plant material, weighed and then placed in cylindrical PVC pots 8 cm in diameter and 10 cm high. Each pot contained about 1 g of leaves. The pots were closed at each end by nylon cloth with a mesh size of 35 μm.

Installation at the study site: Seven series of ten pots corresponding to seven collection dates were placed at the study site and lightly pushed into the litter, with the bottom resting on the H layer so that the leaves were rehumidified before the larvae were introduced. After a week, half of the pots in each series received 200 fourth instar larvae of *B. confinis* (labelled SCIAR). The number corresponds to the average size of a naturally occurring larval cluster. The other five pots contained only leaves (labelled CONTROL). All the pots were removed on April 16, when larval feeding activity had stopped (larvae pupating). The leaves were then put into direct contact with the H layer without any horizontal discontinuity with the surrounding litter. The first two series were taken at 15 days intervals, and the rest at intervals of one month, up until mid-November 1983.

Sampling techniques: Each core was split in two depths: "experimental" leaf layer (eaten or not) and the underlying H layer. The microarthropods were extracted by the Tullgren dry funnel method. Both adult and juvenile individuals were taken into account.

Description of leaves consumed and of faeces produced: The appearance of the eaten leaves and faeces has already been described (Deleporte 1981). The microbiological study of ingested leaves and faeces reveals an abundance of fungal spores and bacteria, in the order of $10^8 g^{-1}$ at the end of February (established by suspension-dilution method and growth on nutrient broth and malt medium) (Deleporte 1988). The broken-down substrate resulting from larval activity is made up of a mixture of particles ingested and then eliminated (faeces) and particles not ingested but crumbled in the course of feeding.

Statistical analysis

Multivariate analysis under linear constraints-principles and application: These methods relate a table Y of dependent variables (e.g. species/samples) to a table X of independent variables which enables explanation of a species table Y; the table X may contain quantitative variables (habitat parameters, litter depth, C/N) or quantitative variables such as the structural variables which reflect a sampling design (date, site, layer). Analysis of coupled tables playing a disymmetrical (as in regression) role may provide answers to two questions in particular:

1 – what is the influence of external variables on the species composition observed in table Y?

2 – what is the optimal ordination of table Y variables considering only the influence of the structure contained in table X (i.e. ordination of species according to sampling site only)?

If table X consists of categorical variables only, one can introduce analysis of variance, with interactions and partitioning of variance; categorical variables are the factors in the ANOVA sense. In our study, table Y is made up of dependent variables: species as columns and replicates as rows. Table X is here made up of disjunct categorical variables reflecting the sampling design: treatment (T), date (D), layer (L). These external variables are also named structure variables.

Principal Component Analysis with Instrumental Variables (PCAIV) in which inertia (or variance) related to each source of variation (T, D, L) is split along the factorial axes (Sabatier et al. 1989, Lebreton et al. 1991) is also named "Redundancy Analysis" by Jongman et al. (1987) & Borcard et al. (1992). Multivariate analysis are carried out with BIOMECO program (Lebreton et al. 1987). We test statistical significativity of PCAIV results by permutation tests (CANOCO program, Ter Braak 1988).

Split plot ANOVA: The data for each species were submitted to a three-way ANOVA of the split-plot type. This analysis is in fact a repetition of univariate-related tests, and for this reason the requirements for applying significance tests are not fulfilled. Therefore, this analysis is presented only for comparison with PCAIV results.

Sampling design: The sampling design is organised as follows: 2 treatments T (SCIAR and CONTROL), 7 dates D, 2 layers L (Leaves and Humus) and 5 replicates per sample (combination "Treatment. Date"). Treatment, date and layer are the external variables whose effects on table Y are evaluated. The sampling design is of the split-plot type: each replicate is subdivided into two layers (leaves and humus).

We use Principal Component Analysis with Instrumental Variables (PCAIV): in this case the dependent variables (species numbers) are considered as measurements. Dependent variables were transformed ($\log(x + 1)$) and normalized. The sampling was carried out according to a fully orthogonal design, for which PCAIV is the most appropriate analysis; it allows the additivity of the different components of the inertia (and their relationships to the external variables) to be preserved. It also permits immediate comparison with a standard ANOVA. Univariate ANOVA of the factorial split-plot (Damon 1987) was also carried out using the main species. Results of this analysis are only given for comparison with PCAIV.

Results

Overall numerical analysis of the oribatid community

Of the 49 oribatid species counted in the whole experiment, 22 were present in large enough numbers (over 30 ind.) for statistical analysis. One of these (*M. minima*) had to be excluded, since its distribution is dependent on pine needles. The remaining 21 species (Table 1) are present both in SCIAR and CONTROL; the dominant species, *O. nova*, *N. silvestris* and *T. velatus* represent, in both cases, between 50% and 60% of the total numbers. An analysis based on total numbers appears insufficient to show any differences, if present, between the two situations (ANOVA on Treatment effect, $p = 0.899$). It does not take into account the responses of the individual species or the interactions between the treatment and the other external variables (date and layer), as does multivariate analysis.

Table 1. Species numbers in CONTROL and SCIAR. Species are ranked according to their decreasing abundance percentage in the SCIAR modality. PAP: small size panphytophagous; PAG: large size panphytophagous; MA: macrophytophagous; MI: microphytophagous

Species		Numbers			Percentage in "SCIAR"	Diet
		Code	CONTR	SCIAR		
Oppia ornata	(Oudemans, 1900)	OPR	11	30	73	PAP
Ophidiotrichus sp.		OPH	12	29	71	PAP
Nanhermannia coronata	(Berlèse, 1913)	NHC	152	300	66	PAG
Platynothrus peltifer	(C. L. Koch, 1839)	PYP	14	25	64	PAG
Hermannia gibba	(C. L. Koch, 1840)	HMG	257	447	63	PAG
Nanhermannia nanus	(Nicolet, 1855)	NHN	52	87	63	PAG
Rhysotritia duplicata	(Grandjean, 1953)	RHD	190	267	58	MA
Oppia obsoleta	(Paoli, 1908)	OPO	90	124	58	PAP
Oribatula tibialis	(Nicolet, 1855)	ORT	364	493	58	MI
Steganacarus sp.		SG1	137	153	53	MA
Chamobates borealis	(Tragardh, 1902)	CHB	377	407	52	PAP
Nothrus silvestris	Nicolet, 1855	NOS	1223	1216	50	PAG
Tectocepheus velatus	(Michaël, 1880)	TVE	1196	1106	48	PAP
Banksinoma lanceolata	(Michaël, 1887)	BKL	197	171	46	PAP
Malaconothrus monodactylus	(Michaël, 1888)	MAM	65	56	46	MI
Oppiella nova	(Oudemans, 1900)	OLN	1778	1495	46	MI
Xenillus tegeocranus	(Hermann, 1804)	XET	28	23	45	PAG
Neotrichoppia confine	(Paoli, 1908)	NEC	230	158	41	MI
Adoristes poppei	(Oudemans, 1908)	ADP	29	19	40	PAG
Quadroppia pseudocircumita	Minguez et al. 1985	QUP	87	47	35	MI
Ceratoppia bipilis	(Hermann, 1804)	CEB	58	25	30	MI
			6547	6678		

Inertia partitioning of species table: The inertia (variance) contained in the species table is split into fractions explained by the different external variables of the experimental design: treatment, Date and Layer. The inertia of the complete model consisting of the principal effects of the variables and of the effects of their interactions, represents 53% of the total inertia, in contrast to 47% unexplained variation (Table 2). The explained inertia is large, considering that the data are the result of random sampling.

The inertia due to the "Total Treatment" (TT) effect is composed of the "Treatment" (T) effect and its interactions with the variables "Date" (D) and "Layer" (L). "TT" represents around 7% of the total inertia (or 14% of the explained variation). The "TT" effect is therefore weak overall (when all species are considered) but this result is not surprising since the variables "Layer" and "Date" play such a predominant role in the overall variation.

Table 2. Partitioning inertia according to the subspaces induced by the structure variables

Source	Dimension of Sub-Space	Inertia	$\frac{\text{PCAIV inertia}}{\text{total inertia}} \times 100$
Treatment (T)	1	0.244	1.16
Date (D)	6	3.929	18.72
Layer (L)	1	3.766	17.94
Interactions			
T.D	6	0.660	3.14
T.L	1	0.087	0.41
D.L	6	1.947	9.27
T.D.L	6	0.546	2.60
Total Treatment (TT)		1.536	7.32
Complete model	27	11.178	53.24
Error	112	9.817	46.76
Total	139	21	100.00

Contribution of species to structure variables: H. gibba alone explains 13% of the variation due to the "TT" effect (Fig. 1). Seven other species show an above-average contribution (4.5%): *X. tegeocranus, A. poppei, O. tibialis, Steganacarus* sp., *N. nanus, O. ornata* and *Ophidiotrichus* sp. Six species have a contribution arount 4%: *P. peltifer, C. bipilis, B. lanceolata, Q. pseudocircumita, N. coronata* and *R. duplicata*. The remaining species have a decreasing contribution from 3 to 1%: *N. confine, C. borealis, O. nova, O. obsoleta, T. velatus, N. silvestris* and *M. monodactylus*.

PCAIV of sub-space "Total Treatment" (TT): At this stage of the analysis, we only consider the sources of variation associated with the effect "Total Treatment" (TT). PCAIV is carried out where the table X is made up only of the variable "Treatment" and its interactions with "Date" and "Layer". Thus the model can be expressed as: TT = T + T.D + T.L + T.D.L.

The first eigenvalue is 0.359, or 23.3% of TT inertia. In total, the first five axes of the PCAIV explain 70.4% of this inertia (Table 3).

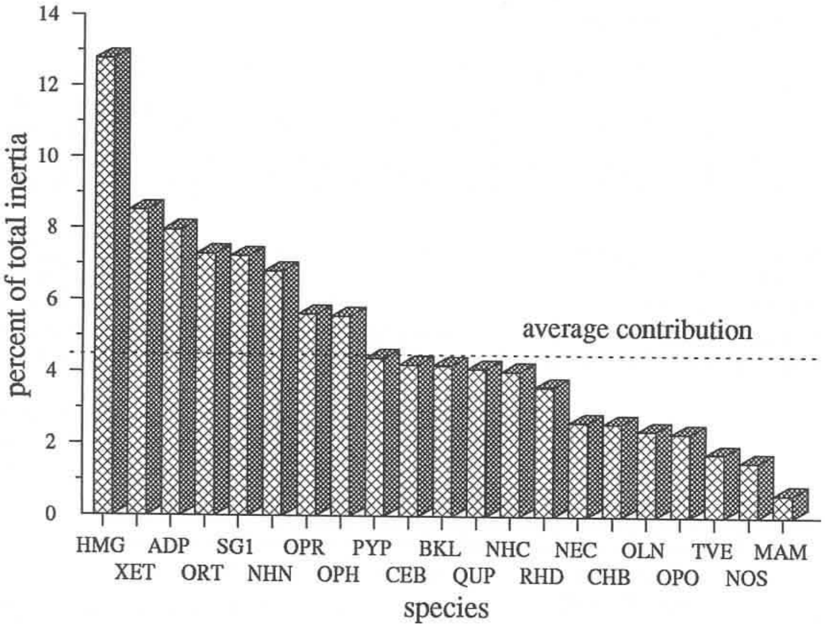


Fig. 1. Contribution of species to "Total Treatment" (TT) (see Table 1 for species code)

Table 3. Importance of PCAIV axes for species: relative contribution of axes to species. The bold numbers represent maximum value for each species. R^2: percentage of variation of each species explained by "Total Treatment"

Species	F1	F2	F3	F4	F5	Rest	Total	R^2 ($\times$ 1000)
HMG	**665**	99	0	50	89	96	1000	197
OPH	**506**	20	79	0	189	206	1000	86
CEB	**457**	50	20	10	**328**	136	1000	65
OPR	**437**	149	0	89	99	226	1000	86
NHC	**298**	99	0	79	**407**	116	1000	62
NHN	**278**	149	209	20	40	305	1000	105
SG1	228	**357**	20	199	99	97	1000	111
XET	99	**576**	50	40	20	216	1000	131
ADP	60	**367**	79	30	10	454	1000	123
PYP	70	**328**	238	40	40	285	1000	68
QUP	30	50	**477**	40	30	374	1000	63
OPO	0	0	**467**	20	20	494	1000	35
NEC	0	0	**437**	79	0	484	1000	40
OLN	20	0	**377**	30	30	543	1000	36
ORT	50	99	30	**576**	30	216	1000	112
MAM	199	10	0	20	298	**474**	1000	10
BKL	60	30	248	109	79	**474**	1000	65
RHD	30	139	60	0	10	**762**	1000	55
CHB	20	129	99	60	10	**682**	1000	40
TVE	10	30	248	0	0	**712**	1000	27
NOS	10	139	20	20	0	**811**	1000	23
INERTIA	0.359	0.276	0.177	0.142	0.130	0.455	1.539	
% TT inertia	23.3	17.9	11.5 **70.4%**	9.2	8.4	29.6	100.0	

Importance of PCAIV axes for species (Table 3):

a) Six species are correlated with axis 1: *H. gibba*, *Ophidiotrichus* sp., *C. bipilis*, *O. ornata*, and to a lesser extent *N. coronata* and *N. nanus*;

b) Four species are correlated with axis 2: *X. tegeocranus*, *A. poppei*, *Steganacarus* sp. and *P. peltifer*;

c) Four species are correlated with axis 3: *Q. pseudocircumita*, *O. obsoleta*, *N. confine* and *O. nova*;

d) *O. tibialis* is correlated with axis 4;

e) *C. bipilis* and *N. coronata*, previously correlated with axis 1, are also correlated with axis 5;

f) Six species are not correlated with any of the first five axes: *M. monodactylus*, *B. lanceolata*, *R. duplicata*, *C. borealis*, *T. velatus* and *N. silvestris*.

Correlation between the variable "Treatment" and PCAIV axes (Tables 4, 5)
Permutation tests show that only principal effect "Treatment" (T) and interaction "Treatment. Date" are significant. The qualitative variable "Principal Treatment" (T) is strongly correlated with axes 1 and 3, and clearly less with axis 2. Some modalities of variable "Treatment. Date" are well correlated with the first three ordination axes, and some others are strongly correlated with axis 5.

Table 4. Correlation between "Treatment" and "Treatment. Date" vs PCAIV axes (cf. Fig. 3b and 4b). CONTROL modalities are not figured (same value than SCIAR but opposite sign)

	F1	F2	F3	F4	F5
Treatment					
SCIAR	−0.69	−0.25	−0.51	−0.10	−0.02
Treatment. Date					
SCIAR/Apr.	0.18	0.06	−0.16	−0.02	−0.23
SCIAR/May	0.19	−0.14	−0.36	−0.34	0.20
SCIAR/June	−0.06	0.04	−0.06	0.09	0.42
SCIAR/July	−0.35	0.50	0.17	0.35	−0.08
SCIAR/Sept.	−0.36	−0.21	0.53	−0.30	0.23
SCIAR/Oct.	0.46	−0.13	−0.04	0.04	0.15
SCIAR/Nov.	−0.05	−0.11	−0.08	0.17	−0.69

Table 5. Significance tests of PCAIV results, using permutation methods

SOURCE	Trace of PCAIV	Percentage	Permutation test	
			F-Ratio	Probability
Principal effect:				
Treatment (T)	0.244	1.16	2.75	<0.001
Interactions:				
Treatment. Date	0.659	3.14	1.11	0.04
Treatment. Layer	0.086	0.41	0.98	0.49
Treat.Date. Layer	0.548	2.61	1.04	0.39
Global effect	1.537	7.32	1.26	0.04

Ordination of species: The factorial planes are interpreted using the projections of the centroids of the structural variables of which "T" and "T. D" are the most relevant (see above).

a) *Plane 1–2* (Fig. 2) – We distinguish two predominant, almost orthogonal, axes represented respectively by the two centroids of the variable "T" (SCIAR and CONTROL) and by two centroids of the variable "T. D" (SCIAR/JULY and CONTROL/JULY). We note the orientation in opposition along the axis SCIAR ↔ CONTROL of *H. gibba* and *C. bipilis*, and along the axis SCIAR/JULY ↔ CONTROL/JULY of *A. poppei* and *X. tegeocranus*.

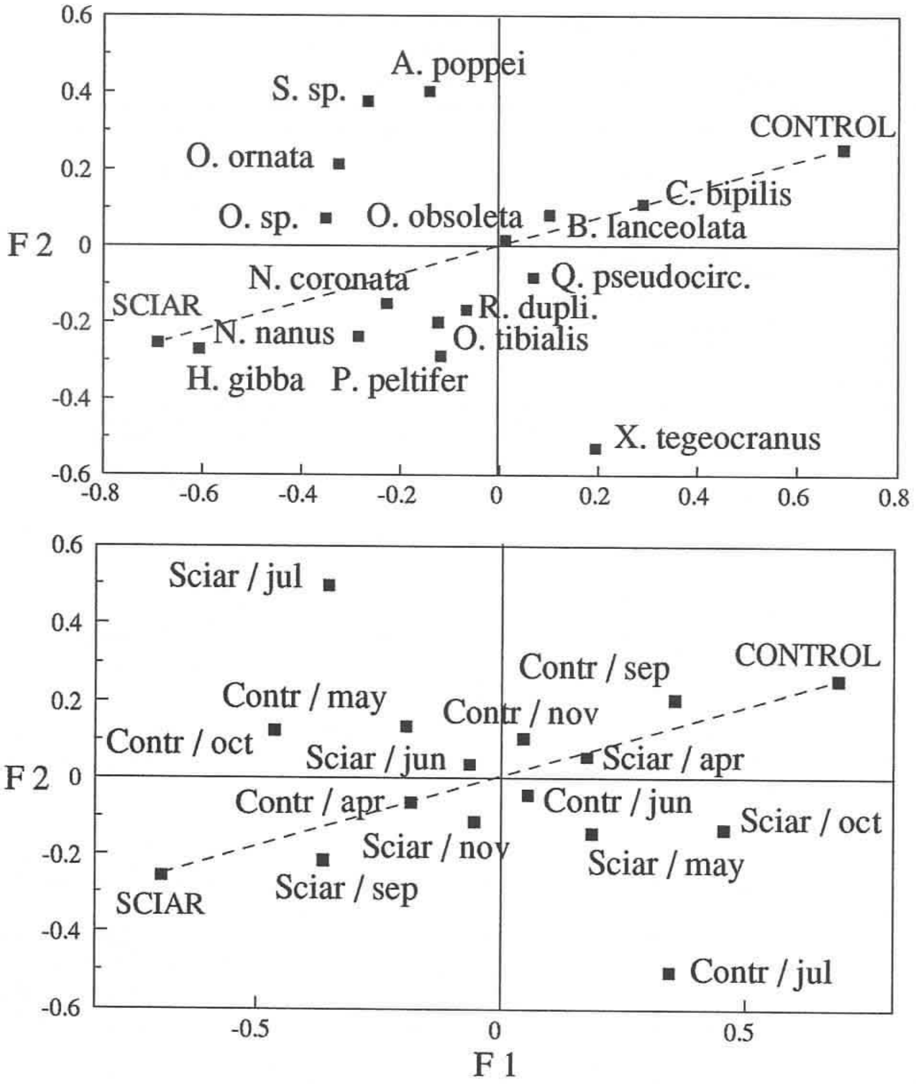


Fig. 2. Ordination of species according to the plane F1–F2 of PCAIV (a) and the variables "Treatment" and "Treatment.Date" (b) (for a clearer reading, the species located at the centre of the graph are not represented)

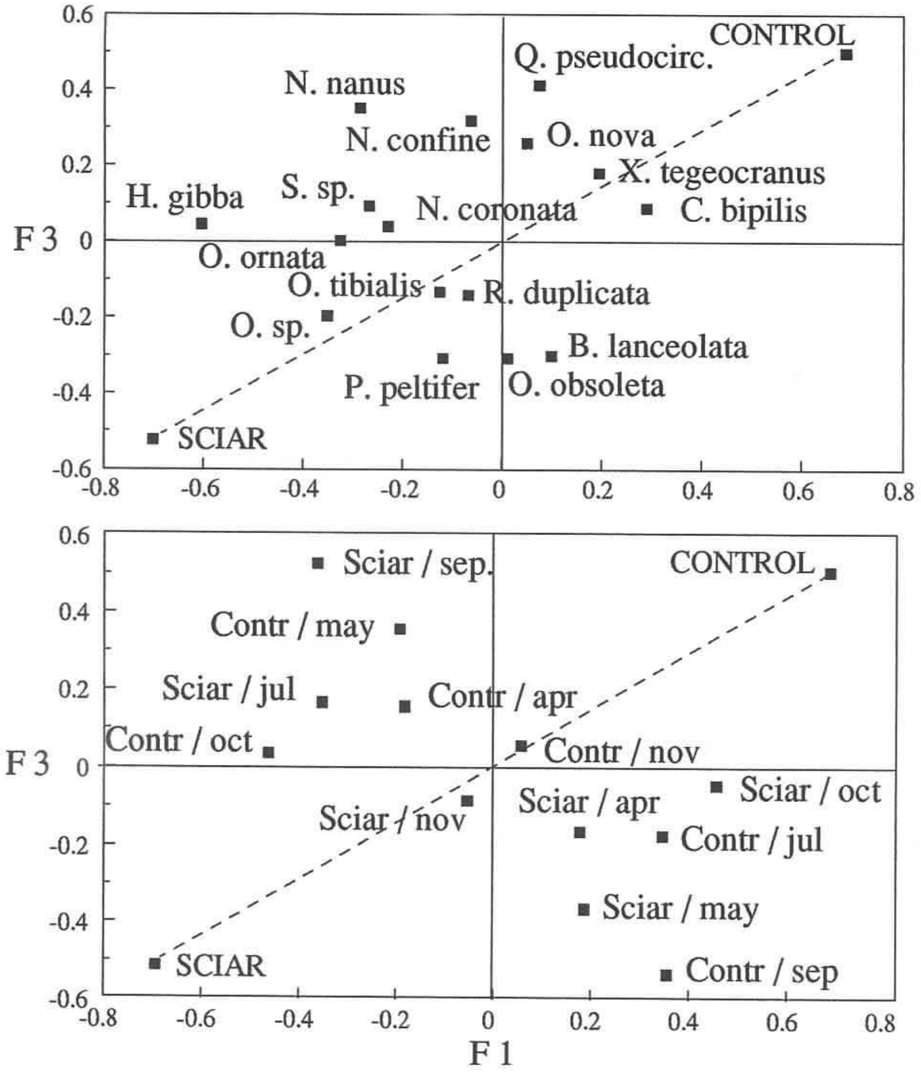


Fig. 3. Ordination of species according to the plane F1–F3 of PCAIV (a) and the variables "Treatment" and "Treatment.Date" (b) (for a clearer reading, the species located at the centre of the graph are not represented)

b) *Plane 1–3* (Fig. 3) – This plane clearly distinguishes an axis "Treatment" and an axis "Treatment. Date". The two dominant directions are represented by the two centroids of the variable "T" and two other centroids of the variable "T. D": SCIAR/SEPT ↔ CONTROL/SEPT. Species for which the principal effect is important are the following: *H. gibba*, *C. bipilis*, *Ophidiotrichus* sp., *O. ornata* and *N. coronata*. Species related to the interaction "T. D" are *N. nanus*, *O. obsoleta*, *Q. pseudocircumita*, *O. nova* and *N. confine*.

Projection of the sub-space defined by the axes F1 to F5 on the variable "T" (Fig. 4): This projection ranks species according to their position on the first five axes of the PCAIV. From the preceding information, we select 16 species which can be classed in the following manner:

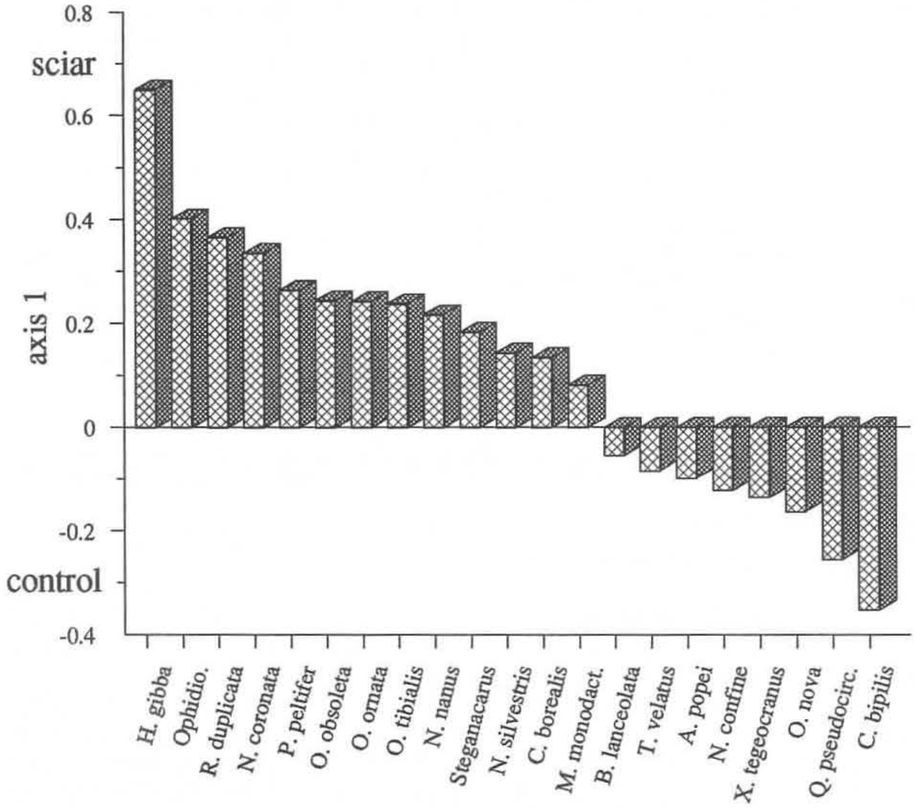


Fig. 4. Ordination of species after projection of the sub-space defined by the axes F1 to F5 of PCAIV on the variable "Treatment"

1. Species strongly associated with the principal effect:
* positive association: *H. gibba*, *Ophidiotrichus* sp., *O. ornata*, *P. peltifer*, *N. coronata;*
* negative association: *C. bipilis*;

2. Species associated with the strong interaction component "T. D" (September numbers):
* positive association: *N. nanus*, *O. obsoleta;*
* negative association: *Q. pseudocircumita*, *O. nova*, *N. confine;*

3. Species whose variation is mostly explained by the "T. D" interaction (July numbers): *Steganacarus* sp., *A. poppei*, *X. tegeocranus;*

4. Particular cases:

O. tibialis is classed among the species strongly correlated with the SCIAR effect, but as a unique abundance profile (associated with axis F4); *R. duplicata* (code RHD) is classed as one of the species most correlated with the SCIAR effect (see Fig. 4), even though it is not prominent on the axes F1 to F5 (see Table 3).

Split-plot ANOVA

The data for each species were submitted to a three-way ANOVA of the split-plot type. Among the 16 species retained in the multivariate analysis, ANOVA gave significant results for the effect of the "Treatment" factor in the case of eight species, either as the principal effect or in interaction with other factors (Table 6):

Table 6. Split-plot ANOVA. Univariate F-test significativity: (*) = test significant at $p < 0.05$; (**) = test significant at $p < 0.01$; (***) = test significant at $p < 0.001$; (!) = p near 0.05

	DATE	LAYER	D*L	TREAT	T*D	T*L	T*D*L
H. gibba	***	!	***	**	*	!	*
O. tibialis	***	**	***	!	!	**	NS
N. coronata	***	***	***	**	NS	NS	NS
Ophidiotrichus sp.	NS	**	NS	*	NS	NS	NS
Steganacarus sp.	***	NS	***	NS	**	NS	NS
C. bipilis	***	***	*	*	NS	NS	NS
Q. pseudocircumita	***	***	***	NS	NS	!	NS
X. tegeocranus	**	NS	NS	NS	NS	NS	*

1. Five species respond to the presence of a substrate transformed by sciarids: *H. gibba*, *Ophidiotrichus* sp. and *N. coronata* respond positively, whereas *C. bipilis* and *Q. pseudocircumita* respond negatively.
2. *O. tibialis* behaves in a unique way: its response to the "Treatment" effect varies depending on the layer considered (leaves or humus).
3. Two species, *Steganacarus* sp. and *X. tegeocranus* show a strong contribution to interactions and a weak response to ANOVA. For these species the effect of "Treatment" is only shown on one or two particular dates. In the case of *X. tegeocranus*, the results show a three-way interaction which is difficult to interpret.
4. Eight species give results which are not significant in univariate ANOVA: *O. ornata*, *P. peltifer*, *O. obsoleta*, *O. nova*, *N. confine*, *A. poppei*, *N. nanus* and *R. duplicata*. In the case of *O. ornata* and *P. peltifer*, the numbers are probably too low. Their positive response needs to be confirmed. In the other cases, the nonsignificance is probably explained by a high intra-sample variability.

Temporal correlation between the two situations

All species show more or less marked seasonal cycles. If we put forward the hypothesis that the temporal variations in abundance linked to the development cycle are the same in either experimental situation we should see a strong correlation between populations in both SCIAR and CONTROL. Conversely, if the fluctuations are not synchronised in the two situations the correlation would be weak. Here we use the Spearman coefficient of correlation (r_s).

1. Species associated to Treatment:
   a. *H. gibba* (low r_s) (Fig. 5a): the "Treatment" effect interferes with the "cycle" effect to the extent of obscuring seasonal periodicity; the difference between eaten and uneaten leaves is at a maximum in the middle of the period of the study;
   b. *O. tibialis* (average r_s): the difference between the two situations is particularly obvious at the beginning of the experiment (Fig. 5b);
   c. *N. coronata* (high r_s) is clearly influenced by the action of sciarids but the "Treatment" effect is expressed by an increasing difference at the very end of the experiment (Fig. 5c).
   Each of these species shows a period of maximum colonization of eaten leaves: *O. tibialis* is early, *H. gibba* is in the middle and *N. coronata* is late.
2. Species not associated to the Treatment: in *O. nova*, the developmental cycle is short (about a month; Woodring & Cook 1962), which explains the lack of periodicity (low r_s) (Fig. 5d). Conversely, *T. velatus* (Fig. 5e), *B. lanceolata* ($r_s = 0.79$) and *C. borealis* ($r_s = 0.74$) show strong synchronisation in the fluctuations of their populations (high r_s).

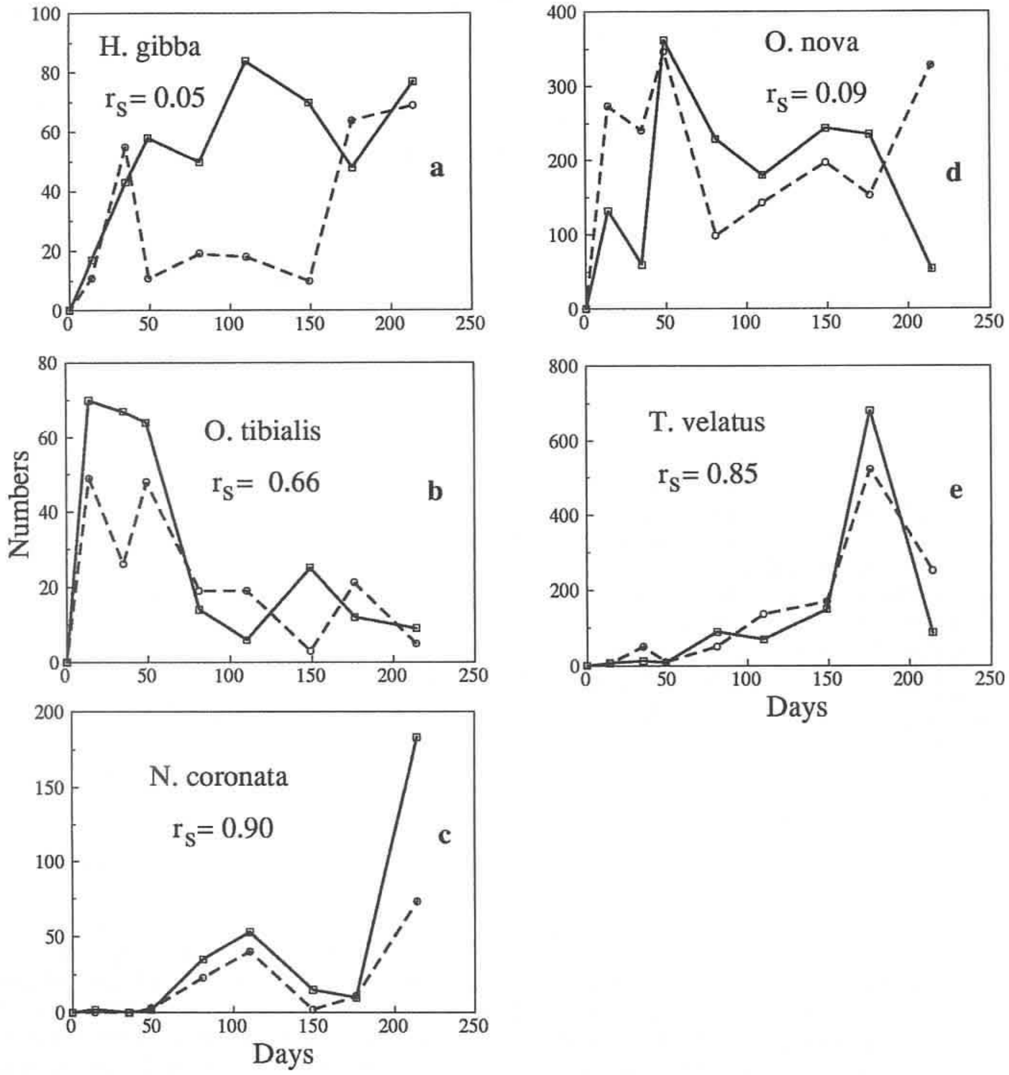


Fig. 5. Temporal correlation between the two situations; r_s: Spearman coefficient of correlation (□——□ = SCIAR; ○– –○ = CONTROL)

Vertical distribution

If we rank the 21 species studied in decreasing order according to their percentage presence (relative to total numbers) in the leaves, there are eight species over 50% and eleven species lower than 22%. Two species fall between these two groups: *C. borealis* (48.6%) and *B. lanceolata* (38.8%). We rank the first eight as litter-dwellers and the last eleven as humus-dwellers (Table 7).

From Table 7, we can see that the results from the analysis of litter-living species are not linked to their vertical distribution. It seems, however, that with humus-dwellers species the percentage in the leaves is consistently higher since the response to "Treatment" is positive. However, these results are from small samples and thus may only indicate general tendency.

Table 7. Vertical distribution of the species according to their percentage in the leaves and their response to "Treatment" effect; – – for the more strongly negative effect to + + for the more strongly positive effect, 0 for species indifferent to the treatment

Species	%	"Treatment" effect				
		CONTROL – –	CONTROL –	0	SCIAR +	SCIAR + +
Litter-dweller species						
A. poppei	83.3			(*)		
P. peltifer	82.1					*
C. bipilis	80.7	*				
O. ornata	68.3					*
X. tegeocranus	60.8			(*)		
Steganacarus sp.	56.9				*	
H. gibba	55.7					*
O. tibialis	52.9					*
C. borealis	48.6			*		
B. lanceolata	38.8			*		
Humus-dweller species						
O. obsoleta	21.7				*	
N. nanus	18.7					*
Ophidiotrichus sp.	14.6					*
R. duplicata	14.5				*	
N. silvestris	6.6			*		
N. coronata	6.6					*
T. velatus	5.0			*		
O. nova	2.2		*			
N. confine	1.6		*			
M. monodactylus	0.8			*		
Q. pseudocircumita	0.0	*				

1. Species responding to Treatment:

- a. litter-living species: *H. gibba* and *O. tibilias* respond positively to the SCIAR treatment: for *H. gibba* (Fig. 6a), the maximum SCIAR effect observed is explained by a massive colonization of eaten leaves. Their numbers were equally divided between leaves and humus in the CONTROL situation; the species is clearly litter-living in the SCIAR situation. Conversely, *O. tibilias* (Fig. 6b) appears litter-living in the CONTROL situation and equally distributed in the SCIAR situation. During spring, this last species lives mainly in humus. *C. bipilis* (Fig. 6c) is a large litter-living species which colonizes the leaves at the beginning of experiments; at this time, we find it mostly in uneaten leaves.
- b. humus-dweller species: *N. coronata* (Fig. 6d) is humus-dweller and responds positively to "Treatment" at the end of the experiment; no temporal fluctuation in vertical distribution was observed; *Q. pseudocircumita* is strictly humus-dweller (all individuals were collected in the humus layer) but has a negative response to "Treatment".

2. Species unaffected by "Treatment": *Steganacarus* sp. and *N. silvestris* are litter- and humus-dwellers, respectively (Fig. 6e, f).

Diet (Table 1)

Adapting the classification of Schuster (1956) & Luxton (1972) used notably by Behan-Pelletier & Hill (1983) and Kaneko (1988), four categories are distinguished:

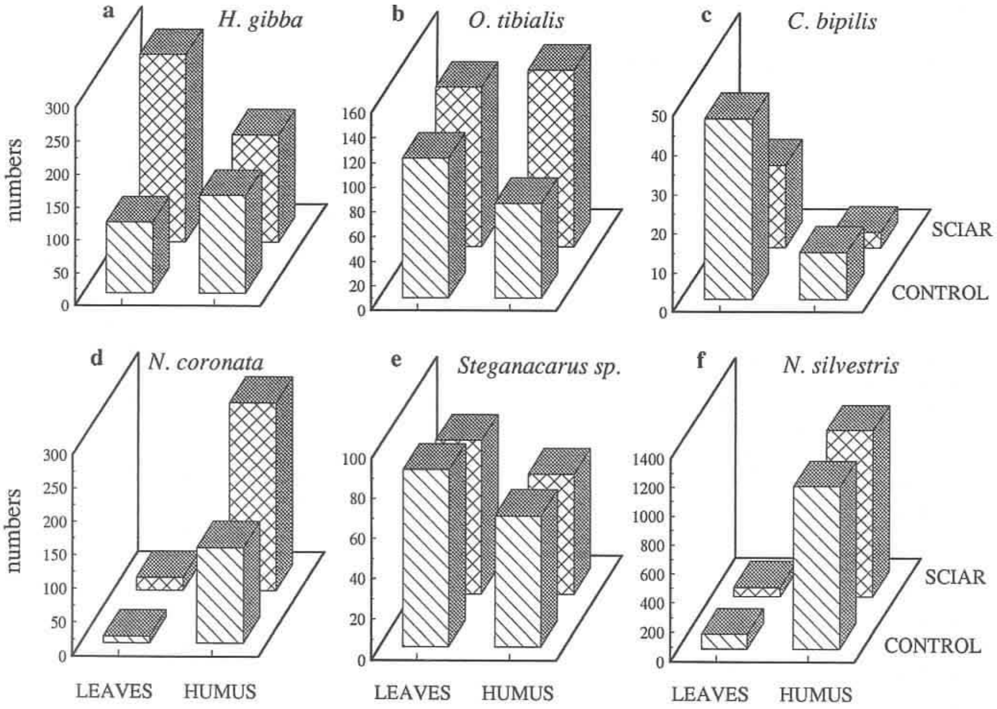


Fig. 6. Overall response of species to "Treatment" in the two layers considered

- macrophytophagous (MA) which eat large leaf fragments (two species),
- large panphytophagous (PAG) which eat large particles of leaves and fungi (seven species),
- small panphytophagous (PAP) which eat small particles of leaves and fungi (six species),
- microphytophagous (MI) which only eat microscopic fungi and bacteria, mycelia and spores (six species).

If we rule out *A. poppei* and *X. tegeocranus* (for which we have already described an unusual response in our analysis), we note that the macrophytophagous (*Steganacarus* sp. and *R. duplicata*) and large panphytophagous (*H. gibba*, *N. coronata*, *N. nanus* and *P. peltifer*) respond rather positively to the treatment; the small panphytophagous (*C. borealis*, *B. lanceolata* and *T. velatus*) are unaffected; the microphytophagous (*C. bipilis*, *O. nova*, *N. confine* and *Q. pseudocircumita*) respond negatively, *O. tibialis* being an exception. These results, as with the preceding point, only indicate a tendency, all the more so since only adults are taken into account in the diet categories.

Discussion

Taken as a whole, the oribatid communities are almost identical, both in density and species composition in the two experimental situations. However, the detailed analysis at a specific level, using multivariate methods under linear constraints, highlights those species that respond positively and negatively to a substrate modified by sciarid fly larvae. Thus, we can synthesise the results about the relevant species (Table 8). We emphasize the relevance of the multivariate methods to make an accurate ordination of these species. Ten species out of 21 significantly respond to leaf breakdown. Among the 11 species which do not react to the treatment, *T. velatus*, *O. nova* and *N. silvestris* dominate the community. Their

Table 8. Synthesis of relevant species according to the different statistical methods

SPECIES	Relevant Species								ANOVA	Cited Species		
	Importance of PCAIV factors					Ordination				Temporal correlation	Vertical distribution	Diet
	F1	F2	F3	F4	F5	Plane 1–2	Plane 1–3	Projection 1 to 5				
Adoristes poppei		*				*		*				
Banksinoma lanceolata										*		*
Ceratoppia bipilis	*				*	*	*	*	*		*	*
Chamobates borealis										*		*
Hermannia gibba	*					*	*	*	*	*	*	*
Malaconothrus monodacty.												
Nanhermannia coronata	*						*	*	*	*	*	*
Nanhermannia nanus	*						*	*				*
Neotrichoppia confine			*				*	*				*
Nothrus silvestris											*	
Ophidiotrichus sp.	*						*	*	*			
Oppia obsoleta			*				*	*				
Oppia ornata	*				*		*	*				
Oppiella nova			*				*	*		*		*
Oribatula tibialis				*				*	*	*	*	*
Platynothrus peltifer		*						*				*
Quadroppia pseudocirc.			*					*	*		*	*
Rhysotritia duplicata								*				*
Steganacarus sp.		*						*	*		*	*
Tectocepheus velatus										*		*
Xenillus tegeocranus		*				*		*	*			
number cited	6	4	4	1	2	4	9	16	8	7	7	14

lack of reaction should be related with the fact that, according to the literature, they are widespread and generalist species.

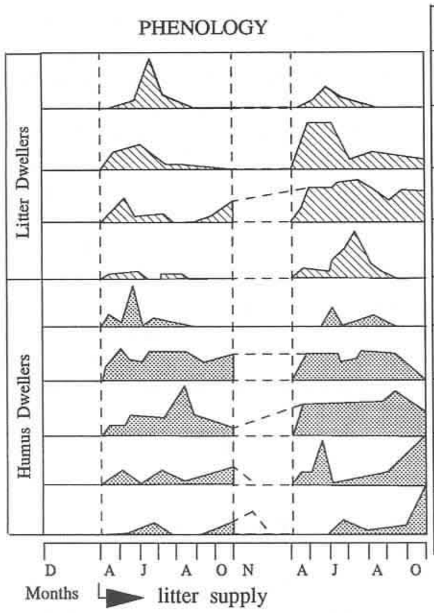
Two aspects of the experimental procedure are particularly important for the interpretation of results. First, preparatory air-drying of the leaves in the experimental pots removed all soil mesofauna; therefore, there was an actual colonization in the L layer starting from zero; this confirms the fact that certain species are attracted or not by the experimental substrates. Second, the humus layer was not modified; the treated leaves were resting directly on the H layer which retained its original fauna. There was no transition layer F.

Thus, colonization by oribatids could happen horizontally through the L layer or vertically from H to L. Among the horizontally-colonizing species (litter-living species), *C. bipilis* is the earliest to appear; it feeds on fungal hyphae which it finds in leaves uneaten by sciarid larvae. *O. ornata* and *H. gibba* appear later and feed on small leaf fragments crumbled by larval feeding action. Among the species which colonize the substrate vertically from the H layer, *O. tibialis* respond quickly and positively to the leaf material crumbled by sciarids. The large increase in its numbers in the H layer is mostly due to the proliferation of immature individuals. *N. nanus* and *R. duplicata* are humus-dwellers and normally feed on degraded material. However, they progressively colonize the L layer as the leaves become more broken down. *N. coronata* is a humus-dweller. The species does not migrate to the L layer, and its positive response to the treatment is delayed until leaf fragments "migrate" to the H layer and become accessible.

In this experiment, we compared simultaneously two states of litter degradation: that of the "L" layer which corresponds to uneaten leaves and that of the "F" layer formed by leaves eaten and fragmented by the larvae. In the natural situation at this site, larval feeding action brings about an acceleration of the maturation of leaf material which in a few weeks passes from an L state to an F state through fragmentation and chemical degradation.

From the experimental results concerning each of the two states L and F studied simultaneously, we have developed a diagrammatic model showing the phases of colonization and succession of several oribatid species on decomposing leaf material in a natural situation (Fig. 7). This diagram is supported by observed spatial and temporal heterogeneity of the litter in the field. We have found (Deleporte 1986, 1987) that *B. confinis* larvae have an aggregated distribution in the litter. Thus areas of leaf litter broken down by larval feeding action and areas of untouched leaf litter are found side by side. Leaves which fall at the same time therefore undergo a different "maturation" depending on whether they pass through the larval gut; this is reflected in the various forms of colonization by oribatids and the diversity of their community. We stress that the homogeneity of the results obtained for populations of certain species over the five replicates for each collection date reflects the homogeneity of the experimental litter, notably the case for species indifferent to the treatment such as *T. velatus*, *N. silvestris* and *B. lanceolata*.

1. Among the litter-living species, we identified four groups characteristic of the successive phases of degradation of leaves in the litter:
   a. early colonizing species;
      - with marked periodicity and found for a certain period only on leaves on the L layer: e.g. *C. bipilis* a microphytophagous species which feeds mainly on unfragmented leaves during the phase of microorganism invasion;
      - with marked periodicity but preferring fragmented leaves: e.g. *O. tibialis*, a microphytophagous species;
   b. species in the middle stages of the succession: *H. gibba* has no marked periodicity; it responds positively to the modified substrate. It shows the same preference for fragmented leaves at the beginning of the experiment (SCIAR situation) and for initially intact leaves at the end of the experiment (CONTROL situation);
   c. late colonizing species: *O. ornata* has a marked preference for leaf material in an advanced state of decomposition.
2. In the humus, the species succeeding one another show similar characteristics. The humus-dwellers, oribatids which respond to the fragmentation of leaves by the larvae,



Species	Stage of Appearance	Phenology	Preferred Troph. Subst.	Diet
C. bipilis	Beginning	Localized	Unfragmented	Micro
O. tibialis	Beginning	Localized	Fragmented	Pan / P
H. gibba	Middle	Diffuse	Fragmented	Pan / G
O. ornata	End	Localized	Fragmented	Pan / P
Q. pseudo.	Beginning	Localized	Unfragmented	Micro
O. nova *N. confine*	Beginning	Diffuse	Unfragmented	Micro
O. obsoleta	Middle	Diffuse	Fragmented	Pan / P
O. sp.	End	Localized	Fragmented	Pan / P
N. coronata *N. nanus* *R. duplicata*	End	Localized	Fragmented	Pan / G

Fig. 7. Schematical representation of phases of colonization and succession of several oribatid species on decomposing leaf material (Micro = microphytophagous; Pan/P = small size panphytophagous; Pan/G = large size panphytophagous)

appear later in the succession (middle and end, respectively *O. obsoleta* and *Ophidiotrichus* sp., *N. coronata*, *N. nanus*, *R. duplicata*), which may correspond to a necessary delay while the elements fragmented at the L layer find their way down to the H layer; moreover, they are panphytophagous species. The species at the beginning of the succession are predominantly humus-dwellers and microphagous (*Q. pseudocircumita*, *O. nova* and *N. confine*). A litter-bag study of Hågvar & Kjøndal (1981) corroborates our results for *O. tibialis* and *O. ornata*. A succession study by Siepel (1990) reports that *N. nanus* colonization reaches a maximum during the end of the first year, whereas a decrease of the numbers is observed during the third year. Thus we must stress that our conclusions are drawn from eight months of observation. Therefore a long-term comparison of both substrates would be of interest. The present study, taking into account both adults and juveniles, emphasized the entire response of each population to the treatment, but it would be interesting to focus on the requirements of the different life stages.

The colonization of these different habitats by oribatid species must be both related to (a) the chemical transformation of leaf material whether fragmented or not, and (b) to their enzymatic capacity to use carbon (notably cellulose) and nitrogen from plant structures (Luxton 1979; Faber 1991). We have already demonstrated the capacity of *B. confinis* larvae to degrade cellulose (Deleporte & Rouland 1991), and have shown that when leaves are eaten by these larvae 50% of the nitrogen is assimilated by the larvae and is therefore less available to developing fungi. This has led us to consider the possibility of competition for nitrogen sources between developing fungi and *B. confinis* larvae (Deleporte 1987, 1988). Competition between the larvae and certain oribatid species (e.g. *C. bipilis*) could also be envisaged.

H. gibba, *O. tibialis* and *C. bipilis* are interesting species concerning the relations between the transformation of leaf material during its degradation and population development. What are the features of the substrate searched by the adults and juveniles using such a substrate degraded by Sciarid larvae? Is it non-ingested (crumbled) leaf particles or ingested particles (faeces)? In fact, the chemical evolution of these two substrates mixed in the litter *in situ* differs according to the presence or absence of enzymatic digestive activity, which in turn regulates the microfloral activity. Future experiments will concentrate on the physico-chemical and microbiological characteristics of the substrate. We will also be able to assess the significance of these new explanatory variables vis-a-vis habitat choice.

Acknowledgments

To J. Travé (CNRS Banyuls/mer) for his invaluable help in the identification of Oribatida, to J. P. Cancela da Fonseca (CNRS Paris VII), J. D. Lebreton (CNRS Montpellier) and R. Sabatier (University of Montpellier) for their advice concerning multivariate analysis, to G. Chaminade and Y. Picard for their technical assistance and to P. Vernon (CNRS Paimpont) for his pertinent comments.

References

Anderson, J. M., Ineson, P. (1982) A soil microcosm system and its application to measurements of respiration and nutrient leaching. Soil Biol. Biochem. **14**, 415–416.

Anderson, J. M., Ineson, P. (1984) Interactions between microorganisms and soil invertebrates in nutrient flux pathways of forest ecosystems. In: J. M. Anderson, A. D. M. Rayner, D. W. H. Walton (eds) Invertebrates – Microbial interactions. Cambridge University Press, Cambridge, pp. 59–88.

Anderson, J. M., Ineson, P., Huish, S. A. (1983) Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. Soil Biol. Biochem. **15**, 463–467.

Behan-Pelletier, V. M., Hill, S. B. (1983) Feeding habits of sixten species of oribatei (Acari) from and acid peat bog, Glenamoy, Ireland. Rev. Ecol. Biol. Sol. **20**, 221–267.

Borcard, D., Legendre, P., Drapeau, P. (1992) Partialling out the spatial component of ecological variation. Ecology **73**, 1045–1055.

Borin, A., Herlitzius, H. (1987) Fluctuations of diptera larvae in soil from a spruce forest in relation to climatic factors. Biol Fertil Soils **5**, 41–48.

Damon, R. A. Jr., Harvey, W. R. (1987) Experimental design, ANOVA, and regression. Harper & Row, Publ., New York.

Deleporte, S. (1981) Peuplement en Diptères Sciaridae d'une litière de chêne. Rev. Ecol. Biol. Sol **18**, 231–242.

Deleporte, S. (1986) Biologie et écologie du Diptère Sciaridae *Bradysia confinis* (Winn., Frey) d'une litière de feuillus (Bretagne intérieure). Rev. Ecol. Biol. Sol **23**, 36–76.

Deleporte, S. (1987) Rôle du Diptère Sciaridae *Bradysia confinis* (Winn., Frey) dans la dégradation d'une litière de feuillus. Rev. Ecol. Biol. Sol **24**, 341–358.

Deleporte, S. (1988) Etude expérimentale de l'ajustement entre le cycle de *Bradysia confinis* (Diptera: Sciaridae) et l'évolution du substract trophique (litière de feuillus): importance des microorganismes. Acta Oecol., Oecol. gener. **9**, 13–35.

Deleporte, S., Rouland, C. (1991) Etude préliminaire de l'équipement digestif osidasique de *Bradysia confinis* (Diptera, Sciaridae): implications dans la dégradation de la matière organique. C.R. Acad. Sci. Paris, III **312**, 165–170.

Faber, J. H. (1991) Functional Classification of Soil Fauna – A New Approach. Oikos **62**, 110–117.

Gunnarsson, T., Tunlid, A. (1986) Recycling of fecal pellets in Isopods: microorganisms and nitrogen compounds as potential food for *Oniscus asellus* L. Soil Biol. Biochem. **18**, 595–600.

Hågvar, S., Kjøndal, B. R. (1981) Succession, diversity and feeding habits of microarthropods in decomposing birch leaves. Pedobiologia **22**, 385–408.

Huhta, V., Haimi, J., Setälä, H. (1991) Role of the Fauna in Soil Processes: Techniques Using Simulated Forest Floor. Agr Ecosyst Environ **34**, 223–229.

Ineson, P., Anderson, J. M. (1985) Aerobically isolated bacteria associated with the gut and faeces of the litter feeding macroarthropods *Oniscus asellus* and *Glomeris marginata*. Soil Biol. Biochem. **17**, 843–849.

Jongman, R. H. G., Ter Braak, C. J. F., Tongeren, O. F. R. van (1987) Data analysis in community and landscape ecology. Pudoc, Wageningen.

Kaneko, N. (1988) Feeding habits and cheliceral size of oribatid mites in cool temperature forest soils in Japan. Rev. Ecol. Biol. Sol **25**, 353–363.

Lebreton, J. D., Roux, M., Bacou, A. M., Banco, G. (1987) BIOMECO – Manuel d'utilisation. Document polycopié. Analyse statistique des processus écologiques, Rte de Mende – B.P. 5051 – 34033 Montpellier Cedex.

Lebreton, J. D., Sabatier, R., Banco, G., Bacou, A. M. (1991) Principal component and correspondence analysis with respect to instrumental variables: an overview of their role in studies of structure – activity and species – environment relationships. In: Devillers, J., Karcher, W. (eds) Applied Multivariate Analysis in SAR and Environmental Studies. ECSC, EEC, EAEC, Netherlands, pp. 85–114.

Luxton, M. (1972) Studies on the oribatid mites of a danish beech wood soil – 1. Nutritional biology. Pedobiologia **12**, 434–6463.

Luxton, M. (1979) Food and energy processing by Oribatid mites. Rev. Ecol. Biol. Sol **16**, 103–111.

Nicholson, P. B., Bocock, K. L., Heal, O. W. (1966) Studies on the decomposition of the faecal pellets of a millipede (*Glomeris marginata* (Villers)). J. Ecol. **54**, 755–766.

Sebatier, R., Lebreton, J. D., Chessel, D. (1989) Principal component analysis with instrumental variables as a tool for modelling composition data. In: Coppi R., Bolasco S. (eds) Multiway data analysis. Elsevier Sciences Publ., North Holland, pp. 341–352.

Schuster, R. (1956) Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. Z. Morph. Okol. Tiere **45**, 1–33.

Setälä, H., Haimi, J., Huhta, V. (1988) A microcosm study on the respiration and weight loss in birch litter and raw humus as influenced by soil fauna. Biol. Fertil. Soils **5**, 282–287.

Shaw, C. H., Lundkvist, H., Moldenke, A., Boyle, J. R. (1991) The relationships of soil fauna to long-term forest productivity in temperate and boreal ecosystems: processes and research strategies. In: W. J. Dyck and C. A. Mees (ed.) Long-term Field Trials to Assess Environmental Impacts of Harvesting. Proceedings, IEA/BE T6/A6 Workshop, Florida, USA, February 1990, pp. 39–77.

Siepel, H. (1990) Decomposition of leaves of *Avenella flexuosa* and microarthropod succession in grazed and ungrazed grasslands. I. Succession of microarthropods. Pedobiologia **34**, 19–30.

Szlavecz, K., Pobozsny, M. (1992) Coprophagy of Diplopods and Isopods: a case for interaction. In: Soil Organisms and Soil Health. Jyvaskyla, Finland, 10–14 August 1992, (in press).

Ter Braak, C. J. F. (1988) CANOCO – an extension of DECORANA to analyze species-environment relationships. Vegetatio **75**, 159–160.

Ter Braak, C. J. F. (1992) Permutation versus bootstrap significance tests in multiple regression and ANOVA. In: K.-H. Jockel, G. Rothe, W. Sendler (eds) Bootstrapping and related techniques. Springer Verlag, Berlin, pp. 79–86.

Woodring, J. P., Cook, E. F. (1962) The biology of *Ceratozetes cisalpinus*, *Scheloribates laevigatus* and *Oppia neerlandica* with a description of all stages. Acarologia **4**, 101–137.